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HEAT LOADS ON REPRODUCING BOBWHITES IN THE SEMIARID SUBTROPICS

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Abstract: The cause-effect process leading to boom-bust population behavior in quails of the semiarid subtropics remains obscure. We challenged the heat hypothesis, which states that heat loads explain variation in quail production among years. Comparison of the 1997 and 1998 breeding seasons in southern Texas revealed the quantity of thermally tolerable space in time (operative temperature $\leq 39^{\circ}\text{C}$) declined and the intensity of thermal conditions increased. This change was associated with an $86.4 \pm 5.43\%$ decrease in the calling activity of northern bobwhite (*Colinus virginianus*) males. We observed heat loads for extended periods within days and breeding seasons and over extensive areas that were sufficient to kill embryos in eggs, chicks, and adults; cause premature incubation and staggered hatching; reduce the length of the laying season and thus inhibit renesting and multiple-brooding; and cause males and females to go out of reproductive condition. Our results supported a necessary condition for the heat hypothesis, namely that thermal conditions severe enough to inhibit quail reproduction occur over extensive areas and times in the semiarid subtropics.

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Key words: *Colinus virginianus*, heat, northern bobwhite, operative temperature, reproduction, temperature, Texas, thermal biology.

Research to understand the cause-effect process governing boom-bust population fluctuations of quails in the semiarid subtropics has been ongoing since the 1940s. Hypotheses on cause that have been rejected because of experimental or empirical counter-instances include variation in vitamin A (Lehmann 1953), phosphorus (Cain et al. 1982), and water nutrition (Guthery and Koerth 1992); variation in intake of reproduction inhibitors (phytoestrogens; Cain et al. 1987); and variation in macronutrition leading to a nonspecific stress response that inhibits reproduction in bust years (Harveson 1995, Radomski 1999).

Although the processes governing boom-bust fluctuations are poorly understood, there is general evidence that precipitation is a strong correlate of quail productivity in the semiarid subtropics. The quantity and pattern of precipitation (or correlated variables) predict production of northern bobwhites (Kiel 1976), California quail (*Callipepla californica*; Francis 1970,

Botsford and Brittnacher 1992), scaled quail (*C. squamata*; Campbell et al. 1973), and Gambel's quail (*C. gambelii*; Swank and Gallizioli 1954, Heffelfinger et al. 1999). Thus, some biotic or abiotic factor that varies with precipitation is implicated in the boom-bust phenomenon.

Research biologists have assumed that the agent causing boom-bust fluctuations is biotic. However, the inhibitory effects of heat (high temperatures) on quail reproduction have been known since the 1930s (Leopold 1933:297). It is also known that heat loads can eliminate the stimulatory effects of rainfall in reproduction by bobwhites (Robinson and Baker 1955) and Gambel's quail (Heffelfinger et al. 1999). Heat apparently suppresses the production of bobwhites in humid subtropical environments (Reid and Goodrum 1960, Speake and Haugen 1960). Guthery et al. (1988) reported evidence that heat reduced the proportion of bobwhite hens laying and males producing sperm, and Guthery (1997) hypothesized that heat acted independently of biotic factors in explaining variation in bobwhite reproduction.

Our purpose was to challenge the heat hypothesis by assaying the nature of heat loads on reproducing bobwhites in the semiarid subtropics (southern Texas). If thermal conditions in breeding areas are sufficiently mild to favor reproduction, regardless of precipitation, then the

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heat hypothesis lacks merit. Conversely, if thermal conditions are severe enough to inhibit reproduction, then the heat hypothesis bears further study. We determined daily and seasonal temperature dynamics on 3 study areas selected for variation in thermal intensity. We also indexed the possible breeding response to thermal conditions with call-counts of bobwhite males.

STUDY AREAS AND METHODS

We selected study sites in Willacy (El Sauz), Starr (El Panal), and Webb counties (Callaghan), Texas, in the Rio Grande Plains. Study sites were about 1, 105, and 167 km (shortest straight-line distance) from the temperature-moderating effects of the Gulf of Mexico. These distances were associated with August mean maximum daily temperatures of 33.9, 36.7, and 37.2°C (Larkin and Bomar 1983). Average annual precipitation was approximately 69, 58, and 56 cm. Thus, expected thermal intensity increased with distance from the Gulf of Mexico.

On each study area we established 3 temperature sampling grids, one each in grassland, low-coverage brushland (10–15% canopy coverage), and high coverage brushland (>25% canopy coverage). We were not interested in the effects of these cover types on heat loads; rather, we wanted to obtain information on the range of thermal loadings that characterized the nesting environment of bobwhites. Each sampling grid consisted of 9 points in a 3 × 3 configuration (25 m between points). Our goal was to sample each grid twice monthly during May–August 1997–98. Sampling began near 0700 and was repeated at 2- to 2.5-hr intervals for a total of 5 sampling periods/day (3 grids × 9 points/grid × 5 samples/day = 135 point-samples/day on a particular study area). Data gathered at each point-sample included soil surface and air temperature at 15 cm aboveground (°C, hand-held digital thermometer), light intensity (lux, hand-held light meter), and wind speed (m/sec, hand-held anemometer). Light intensity and wind speed were sampled at 15 cm aboveground. Sampling revealed little variation and low values for wind speed at this level, so we quit measuring this variable to save time and assumed a wind speed of 1 m/sec in estimating operative temperature. For analytical comparisons between years and among study areas, we used data collected during Julian day 145–220 (25 May–8 Aug). This resulted in a sample of

5–6 series of measurements/study area/year with data well distributed (and hence, comparable) through the period.

We estimated operative temperature (T_e) at 15 cm aboveground with the formula provided by Campbell (1977) and Mahoney and King (1977). Operative temperature (equivalent blackbody temperature) is a better gauge of the thermal environment experienced by an animal than air temperature, because operative temperature takes into consideration the heating effects of solar radiation and the cooling or heating effects of wind. Forrester et al. (1998) gave details on the procedures we followed in estimating T_e . This estimate may be considered the temperature experienced by a spherical object with the dimensions and thermal properties (absorptivity, emissivity) of a Texas bobwhite (*C. v. texanus*).

To derive biological meaning from field data on T_e , we had to establish a landmark temperature for analytical purposes. Bobwhites avoid points in habitat space–time with operative temperatures >39°C (Forrester et al. 1998, Guthery et al. 2000b). This temperature represents the approximate temperature where heat dissipation mechanisms (gular flutter) cannot neutralize the effects of heat gain and body temperature rises (Guthery et al. 2000a). Prolonged exposure to a temperature of 40°C may be lethal to bobwhites (Case and Robel 1974). Thus, we took $T_e = 39^\circ\text{C}$ as an index of the temperature that imposes thermal stress (hyperthermia) on bobwhites; we recognize that any such index is subject to variation among individuals.

We used the landmark temperature to estimate the percentage of points in habitat space–time (Guthery 1997) that were thermally tolerable ($\leq 39^\circ\text{C}$). Space–time implies sampling in space through time. This percentage does not contain information on the intensity of heat loads. Therefore, we found the maximum of mean values for a grid on a Julian day and used the mean of these maximums over 3 grids as an index of thermal intensity. For example, a grid had 9 sample points from which a mean for each of 5 sample periods was calculated. The maximum of these 5 means was determined for each grid. The mean of the 3 maxima (1 from each grid) served as our index of thermal intensity on a Julian day.

We used 1998 data from the El Panal study site to examine the sensitivity of the percentage

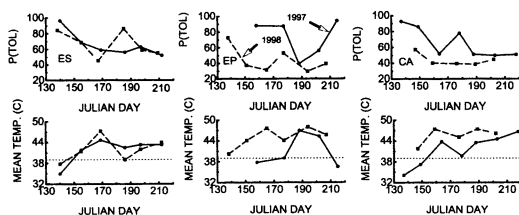


Fig. 1. Temporal trends in the percentage of habitat space-time that was thermally tolerable [$p(\text{tolerable})$, operative temperature $\leq 39^\circ\text{C}$] and on thermal intensity (mean of maximum mean operative temperatures for 3 sampling grids) for 3 study areas in southern Texas, 1997–98. Study area codes and distance from the Gulf of Mexico are ES = El Sauz (1 km), EP = El Panal (105 km), and CA = Callaghan (167 km). The dashed horizontal line is at 39°C . Each point in the graphs is associated with $n = 135$.

of thermally tolerable space-time to the assumption on landmark temperature ($\leq 39^\circ\text{C}$). From the 1998 dataset, we selected the coolest ($T_e = 35.8 \pm 4.30^\circ\text{C}$; $\bar{x} \pm \text{SD}$) and the hottest day ($T_e = 41.0 \pm 7.16^\circ\text{C}$) and estimated the percentage of space-time that was thermally tolerable for 6 temperatures ($39.0, 39.5, 40.0, 40.5, 41.0$, and 41.5°C) on a Julian day over 5 sampling periods and 9 points within a grid. We calculated the means of these percentages for 3 grids with each temperature. We used simple linear regression to estimate the percentage increase in tolerable space-time for each 1°C increase in the landmark temperature.

We established 16-km, 11-stop routes (1.6 km between stops) to index the abundance and calling intensity of bobwhites on each study area. Routes had the same starting and ending points each time they were run. Counts were replicated ≥ 7 times/study area/year during the period 15 May–10 July (1 study area was replicated 8 times in 1 yr). Counts began 0.5 hr after sunrise and ended before 1000 hr. We listened for 5 min at each stop and recorded the number of calls and the estimated number of calling males. We analyzed the number of calling males per route with simple descriptive statistics.

RESULTS

Area and Year Effects

Trends in thermally tolerable space-time and thermal intensity were similar between years on the study area nearest the Gulf of Mexico (Fig. 1ES). The average percentage of thermally tolerable space-time during 25 May–8 August was $59.6 \pm 2.84\%$ (1997; $\bar{x} \pm \text{SE}$) and $62.7 \pm 6.99\%$ (1998); the average thermal intensity indices were 43.1 ± 0.47 and $42.7 \pm 1.37^\circ\text{C}$. Conversely, the

thermal environment was more severe on inland study areas in 1998 than in 1997. Monthly quantities of thermally tolerable space-time were higher during all sampling dates in 1997 than in 1998 and this same general pattern fit the thermal intensity index with 1 exception (Fig. 1ES, 1CA). On the area 105 km from the Gulf of Mexico, the average percentage of tolerable space-time declined from $72.9 \pm 10.76\%$ to $38.0 \pm 4.13\%$ and the mean monthly intensity index increased from $41.1 \pm 2.09^\circ\text{C}$ to $45.9 \pm 0.83^\circ\text{C}$ between 1997 and 1998. Respective values for the area 167 km inland were from $61.2 \pm 6.64\%$ to $43.8 \pm 3.44\%$, and from $42.6 \pm 1.41^\circ\text{C}$ to $45.6 \pm 1.03^\circ\text{C}$. During 1998, the inland areas experienced virtually a complete loss of thermally tolerable space-time in the afternoons after Julian day 150 (30 May; Fig. 1ES, 1CA). Complete loss is indicated, approximately, when the percentage of thermally tolerable space-time reaches 40%, meaning that space-time was tolerable only during the samples taken before noon (2 of 5 sampling periods).

Comparative Dynamics of Air, Ground, and Operative Temperatures

The comparative dynamics of air, ground, and operative temperatures were analyzed for 8 July 1998 on the Callaghan area (167 km from Gulf of Mexico). This day was particularly intense thermally. Early in the day (0800 hr) the 3 temperatures were similar (Fig. 2). By about 1030 hr, ground and operative temperatures started to diverge from air temperature by increasing at a faster rate. Air temperature exceeded the body temperature of quail (41.5°C) from about 1300 through 1630 hr; during this period, any breezes would have added to rather than subtracted from thermal stress. In other words, breezes increase body temperature when air temperature exceeds body temperature. Ground and operative temperatures diverged at about 1300. When ground temperature was below body temperature, the operative temperature experienced by quail was lower than that estimated. This occurred because the ground served as a sump for longwave radiation emitted by quail. Conversely, when ground temperature exceeded body temperature, the ground served as a source of longwave radiation and operative temperature was underestimated.

The dynamics of operative temperature on sampling grids were associated with a threshold-like collapse of thermally tolerable space-time starting shortly after 1100 hr (Fig. 3). All space

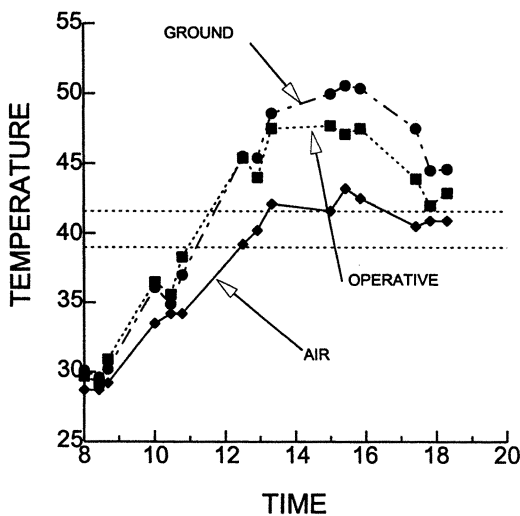


Fig. 2. Dynamics of air, ground, and operative temperature ($^{\circ}\text{C}$) on the Callaghan study area (167 km from the Gulf of Mexico), southern Texas, 8 July 1998. The dashed, horizontal lines represent the approximate body temperature of northern bobwhites (41.5°C) and the approximate operative temperature leading to hyperthermia (39°C). Each point in the graph is associated with $n = 9$.

was thermally intolerable (operative temperature $>39^{\circ}\text{C}$) from about 1230 through 1800 hr (5.5 hr) on Julian day 189 (8 July 1998, Callaghan area).

Landmark Temperature Assumption

On cool days, the estimated percentage of space-time that was thermally tolerable increased at a rate of $10.7 \pm 1.13\%$ for each 1°C increase in the landmark temperature (Fig. 4). The rate of increase was $5.1 \pm 0.36\%$ on hot days. Thus, the percentage of thermally tolerable space-time was more sensitive to the temperature assumption on cool days than on hot days. Biologically, however, the assumption was less critical on cool days than on hot days. On cool days, the availability of thermally tolerable space-time was high and on hot days it was low, regardless of the assumed landmark temperature (Fig. 4). These results imply that our interpretations would have changed slightly had we assumed a landmark temperature of, say, 40°C , which is known to be lethal (Case and Robel 1974).

Activity of Calling Males

The mean number of males heard calling on 16-km routes collapsed on all study areas between 1997 and 1998 (Fig. 5). The average de-

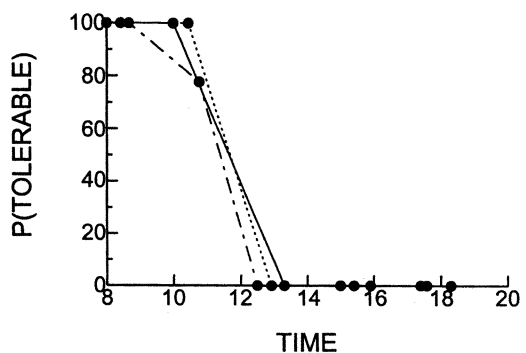


Fig. 3. Daily trend in the percentage of space-time that was thermally tolerable (operative temperature $\leq 39^{\circ}\text{C}$) on 3 heat sampling grids on the Callaghan study area (167 km from the Gulf of Mexico), 8 July 1998. Each point in the graph is associated with $n = 9$.

cline over the 3 areas was $86.4 \pm 5.43\%$. The collapse was particularly strong on the area furthest inland; an average of 10.4 ± 2.37 males in 1997 declined to 0.3 ± 0.18 males in 1998; in other words, calling activity virtually disappeared on the Callaghan area in 1998, coincident with a severe thermal environment (Fig. 1CA).

DISCUSSION

We obtained correlative support that was somewhat ambiguous relative to the heat hypothesis. Data from the coastal area (El Sauz) were not supportive, because the thermal en-

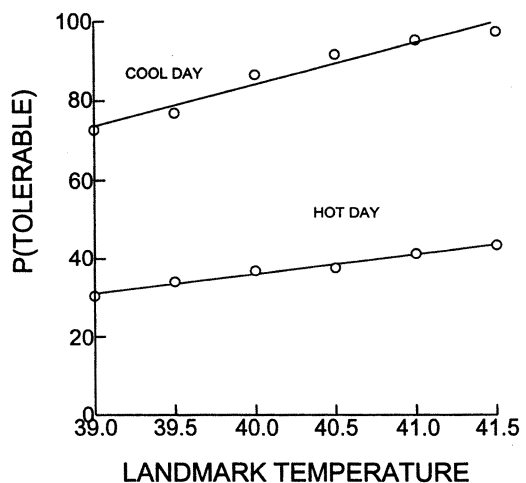


Fig. 4. Sensitivity of the percentage of thermally tolerable space-time [$p(\text{tolerable})$] to the assumed temperature resulting in hyperthermia for northern bobwhites on cool ($T_o = 35.8 \pm 4.3^{\circ}\text{C}$; $\bar{x} \pm \text{SD}$) and hot days ($T_o = 40.0 \pm 7.16^{\circ}\text{C}$), southern Texas, 1998.

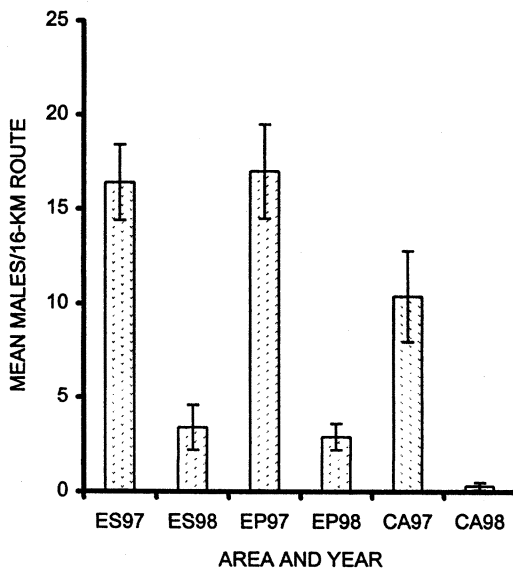


Fig. 5. Variation in the mean number of calling northern bobwhite males heard on 3 study areas in southern Texas during 15 May–10 July 1997 and 1998. Study area codes and distance from the Gulf of Mexico are ES = El Sauz (1 km), EP = El Panal (105 km), and CA = Callaghan (167 km).

vironment, as indexed, was similar between years (Fig. 1ES) and calling activity declined by 79.3% (Fig. 5). The thermal environment was actually less severe on the coastal area in 1997 than in 1998; for example, the thermal intensity index was 44.1°C in mid-June 1997 and 47.2°C at the same time in 1998. Our sampling schedule failed to demonstrate thermal differences that were present between years on the coastal site. On the inland sites, however, an increase in the severity of the thermal environment (Fig. 1EP, 1CA) was associated with an 82.9–97.1% decline in calling activity (Fig. 5).

We cannot rule out the possibility that differences in calling activity between years (Fig. 5) merely reflected differences in population size. We did not have data on population size that were independent from the call index. However, 1997 was regarded as a good production year throughout the southern Great Plains, because of cool, moist conditions known to foster quail production (Robinson and Baker 1955, Heffelfinger et al. 1999). Thus, it seems likely that breeding populations were strong in 1998. Also, the proportion of males that calls may vary with weather variables (Hungerford 1964, Heffelfinger et al. 1999). Thus, our low call count indices in 1998 could have been associated with

relative high populations that were not reproductively active.

Despite uncertainty regarding population status between years, the thermal environments we observed were sufficiently intense to suppress bobwhite reproduction. Blastoderm development in the eggs of bobwhites begins at 24.4–25.6°C (Miller and Wilson 1975) and the typical incubation temperature is about 37.5°C (Wilson et al. 1979). The body mass of laying bobwhites maximizes at about 20.1°C and declines at a rate of 0.17 g/°C for temperatures >20.1°C (derivation from Case and Robel 1974). Based on laboratory studies, net energy devoted to egg production maximizes at 20.9°C and becomes zero at 39.2°C (derivations from Case 1972). Temperatures of 35°C invoke heat dissipation mechanisms (gular flutter) in the laboratory for bobwhites (Spiers et al. 1983) and other quails (Henderson 1971). Operative temperatures in successful nests average 34°C for scaled quail (Evans 1997) and rarely exceed 38.7°C for a variety of birds in southern Texas (Land 1999).

We recorded extended periods within days (Fig. 3) and within the breeding season over extensive areas (Fig. 1) where operative temperatures were >39°C in 1997 and 1998. Based on the thermal biology presented in the above paragraph and previous findings, the thermal environment we observed would be expected to (1) reduce the hatchability of eggs (Leopold 1933:297, Wilson et al. 1979); (2) cause premature incubation and staggered hatching dates (Stanford 1972); (3) result in the production of subnormal chicks (Yeatter 1950), kill young chicks from hyperthermia (Sumner 1935, Evans 1997), or potentially reduce chick survival by inhibiting foraging time (Goldstein 1984); and (4) reduce the length of the laying season (Klimstra and Roseberry 1975, Guthery et al. 1988) and thereby reduce opportunities for re-nesting and multiple-brooding (Guthery et al. 2000a). Adult Gambel's and scaled quail may die within 2 hr when exposed to a temperature of 45°C (Henderson 1971). Thus, we observed thermal conditions potentially lethal to adult birds (Fig. 2). Heat loads would be expected to act on ≥ 7 of 10 variables that govern bobwhite production in any year (Guthery and Kuvlesky 1998:540–541) the proportion of hens that participates in reproduction, the potential number of nesting attempts per hen, effective clutch size, length of the laying season, survival of

chicks and adults, and the proportional distribution of successful nest starts in time.

The heat hypothesis is consistent with the observation that precipitation is predictive of reproductive vigor for quail in the semiarid subtropics. Precipitation would result in increased vegetation cover, moist soil, and evapotranspiration, all of which would ameliorate the thermal environment.

MANAGEMENT IMPLICATIONS

We did not set out to derive management implications from this study; rather, we set out to understand. Understanding leads to management implications, because man masters nature by understanding, not by management force (Bronowski 1965:10).

The heat hypothesis remains provisional. We have demonstrated that it is plausible in some portions of the semiarid subtropics, because the thermal environment may be intense enough during the breeding season to inhibit reproductive function. Further challenges to the hypothesis could involve more detailed analysis of thermal conditions available during the breeding season relative to the behavior of individuals and populations. A useful study would be to determine the thermal environment of successful nests, as Land (1999) has done for nongame birds in southern Texas. Controlled, laboratory studies of bobwhite egg-laying in response to artificial thermal regimes would assist biologists in interpreting field data. Biologists also need to understand the response of reproducing quail to acute versus chronic exposure to high heat loads. Could, for example, a few excessively hot days in an otherwise cool breeding season suppress reproduction for a longer period? A 3-day exposure to intense heat (35°C) resulted in an 8-week suppression of egg-laying performance in domestic poultry (Tanor et al. 1984). Acute exposure to high heat loads might explain our ambiguous results on the coastal study area; i.e., the average thermal environment was similar between years (Fig. 1ES) but the calling activity of males was suppressed in 1998.

Until the heat hypothesis is refuted or accepted, applied ecologists should recognize that mounting evidence indicates bobwhites and probably other quail seem quite sensitive to temperatures. Heat avoidance may explain their field behavior as well as predator avoidance (Forrester et al. 1998). Temperatures lethal to quail occur commonly in the semiarid subtrop-

ics (Goldstein 1984, this study). Thus, management measures, such as reduction or elimination of grazing pressure and preservation of woody cover, that reduce heat loads or provide thermal refugia likely will improve conditions for quail.

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